Cochlear suppression of tones by dynamic stimuli

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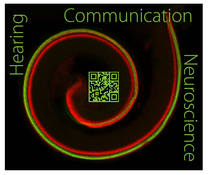

INTRODUCTION

Behavioral studies show that when a tone is presented together with a competing sound, the audibility of the tone can be reduced (i.e., masking). The amount of masking depends on the characteristics of the competing sound. Although masking by sounds with static properties is relatively well explained, **masking by sounds that change dynamically over time (e.g., frequency chirps) is less understood**. For instance, upward linear frequency chirps (i.e., sweeping frequency from low to high) are typically much more effective maskers than downward (high to low sweep) sweeps, especially at lower masker levels. This discrepancy in masker effectiveness occurs only in subjects with normal hearing, suggesting that this phenomenon depends on active cochlear processing (Summers and Leek, 1998). Previously, these puzzling results were interpreted in terms of cochlear dispersion: Upward sweeps augment the effects produced by cochlear dispersion, resulting in cochlear responses that ring longer and produce more masking compared to downward sweeps, which partially compensate for cochlear dispersion and produce more temporally localized responses.

In this study, **we investigate "masking" as seen directly in cochlear vibrations (i.e., suppression) when a tone is presented together with a swept suppressor tone.** Because the cochlear frequency-place map is roughly exponential, we use exponential frequency chirps instead of linear ones. To explore the effect of cochlear dispersion on the strength of suppression, we manipulate the direction of the frequency sweep, as done in behavioral studies, as well as its rate (or, equivalently, the total sweep duration). Mechanical vibrations in a mouse cochlea are measured using optical coherence tomography.

METHODS

Paradigm

Cochlear vibrations were measured in response to a tone presented in isolation and together with a suppressor sweep. The suppressor phase was rotated by 180 degrees on alternate presentations to cancel out the cochlear response to the suppressor stimulus. Suppression was evaluated by calculating the "residual" waveform as the difference between the cochlear response to probe-alone and probe + suppressor conditions. The residual represents the change in the BM response to a probe tone due to the presence of the suppressor.

Probe tone parameters: steady-state tone with frequency set to the characteristic frequency (CF) and level set to 40 dB SPL;

Suppressor sweep parameters: instantaneous frequency of sweep stimulus was varied exponentially between 0.5 and 40 kHz, in upward or downward directions (Fig. 1). The duration of the sweep stimulus was set to either 5, 10, 50, or 100 ms corresponding to sweep rates of 1.26, 0.63, 0.13 and 0.06 octave/ms, respectively. For reference, the rate of instantaneous frequency change of the BM response to a click is about ~1 oct/ms for mice at the apex. The sweep level was set to either 60 or 80 dB SPL.

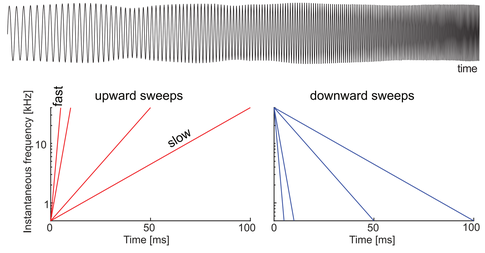

Fig. 1. An example of an upward swept-tone stimulus (top). The sweep instantaneous frequency versus time for different sweep durations used in the experiments (bottom).

Animal preparation and Instrumentation

All experiments were carried out in anesthetized adult mice (CBA/CaJ; n = 8) with ventilated bulla. Stimuli were generated digitally (100 kHz sampling rate) and delivered through the sound sources of the ER10X probe system (Etymotic Research). Basilar membrane (BM) vibrations were measured from ~8-10 kHz tonotopic locations with Optical Coherence Tomography (Gao et al., 2014). Animal care protocols were approved by the USC Institutional Animal Care and Use Committee.

Acknowledgments
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RESULTS Part I

I. Basilar-membrane (BM) response to a sweep stimulus:

Upward fast sweeps evoke longer lasting responses than downward fast sweeps.

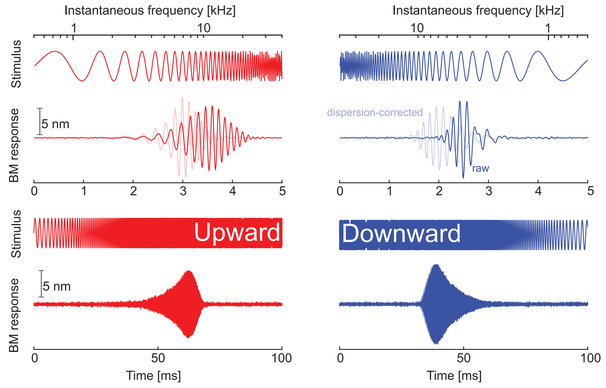

Fig. 2. Examples of BM responses (CF = 9.2 kHz; ID #120621) to upward (red) and downward (blue) 60-dB SPL sweeps of varying durations (5-ms top, 100-ms bottom). The BM responses corrected for cochlear dispersion (i.e., by removing the frequency-dependent BM delay) are shown by the light-colored dotted lines. After correcting for cochlear dispersion, all BM responses peak at the time corresponding to an instantaneous sweep frequency of ~8-9 kHz. Examples of stimulus waveforms are shown above each trace.

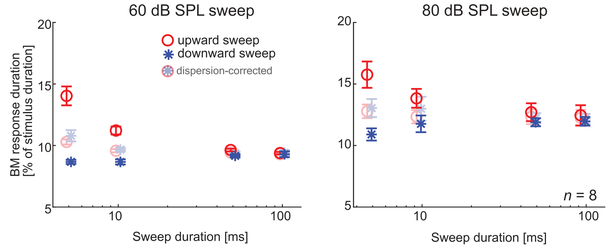

Fig. 3. The average (±95% CI obtained via bootstrapping) BM response duration before (saturated colors) and after (light colors) correcting for cochlear dispersion. The BM response duration was computed as an equivalent rectangular duration of the envelope of the responses showed in Fig. 2 and expressed as percent of the stimulus duration. The effect of sweep direction on the duration of the BM response was abolished post mortem (not shown). The amplitude at peak of the BM response envelope did not vary significantly across the stimulus conditions.

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RESULTS Part II

II. Suppression of a low-level probe tone by a sweep stimulus:

Upward fast sweeps suppress the probe response over a longer time interval than downward fast sweeps.

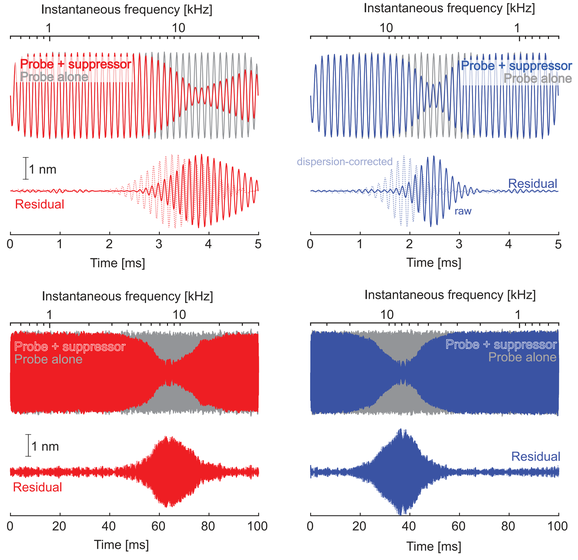

Fig. 4. The BM response to a 40-dB SPL 9.2-kHz probe tone presented alone (gray) or in the presence of a 60-dB SPL suppressor sweep (colored). The difference between the two waveforms (residual response, displayed under each panel) represents a change in the BM probe response caused by the suppressor sweep. (CF = 9.2 kHz; ID #120621)

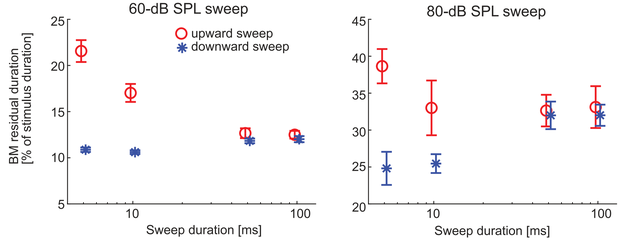

Fig. 5. The average (± 95% CI) duration of the BM residual response (calculated as in Fig. 3). The up/downward sweeps suppress the probe response over longer/shorter time periods for fast but not for slow sweep stimuli.

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SCAN ME

RESULTS Parts III & IV

III. The duration of suppression correlates with the duration of the response to the suppressor sweep:

On average the duration of the residual response was ~1.4 times longer than the duration of the BM response to the sweep stimulus.

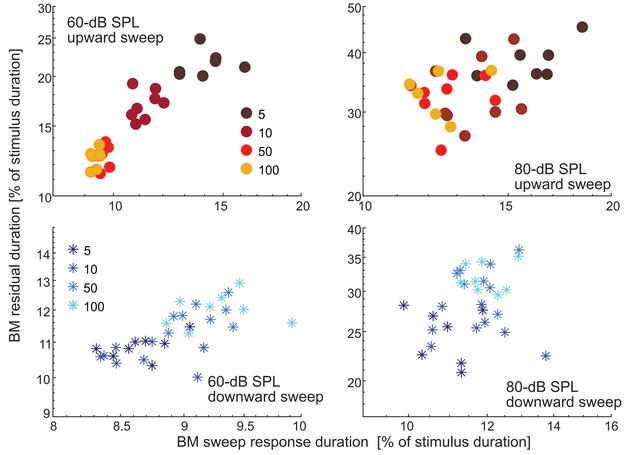

Fig. 6. The change in the residual response duration (i.e., duration of "suppression") as a function of the duration of the BM response to the sweep stimulus of varying levels (left vs. right), directions (up vs. bottom), and duration (colored coded - see the legend).

IV. Frequency tuning of the suppression:

When corrected for cochlear dispersion, slow sweeps accurately predict two-tone suppression tuning. Fast up/downward sweeps over/underestimate suppression on the high-frequency side.

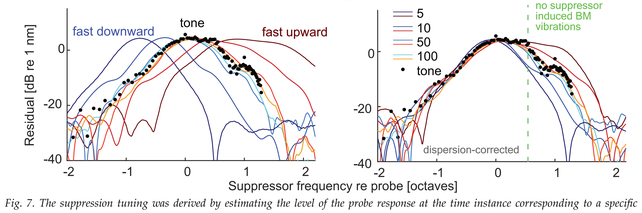

Fig. 7. The suppression tuning was derived by estimating the level of the probe response at the time instance corresponding to a specific suppressor frequency through a Least Square Fit (Long et al., 2008). On the right, the residual waveforms were corrected for cochlear dispersion before applying LSF. The two-tone suppression residual was also measured with a pair of pure tones (black circles). ID#121721.

SUMMARY

- Our results confirm previous observations in chinchillas where linear upward sweep stimuli evoked longer ringing in the BM response than downward sweeps (Recio & Rhode, 2000).
- We further show that this effect persists only when the rate of frequency change of the sweep is comparable with the rate of a cochlear dispersion (fast sweeps; Fig. 3).
- The suppression of the low-level probe response varies in proportion to the duration of the BM response to the sweep stimulus, so that fast upward/downward sweeps caused longest/shortest lasting suppression (Fig. 6).
- The BM response duration to fast sweeps can be corrected for the dispersive effects (Fig. 3, lighter colors). Despite the correction, the fast sweep suppressive effects vary on the high-frequency side of the suppression curve with upward sweep being more effective (Fig. 7).
- These findings confirm that suppression of cochlear amplification and dispersion are most likely the source of difference in perceptual masking by up/downward sweeps in normally hearing subjects.